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INCORPORATING COMPETITION BETWEEN LIFE FORMS INTO
THE SOIL WATER SUBMODEL WITHIN STAND-BGC,
A VEGETATIVE PROCESS MODEL

by

Ellen P. Voth

B.A., Bethel College – North Newton, KS, 1990

Presented in partial fulfillment of
the requirements for the degree of


Master of Science

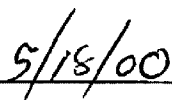
University of Montana, School of Forestry

2000

Approved by:


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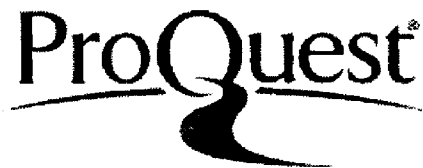


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ABSTRACT

Voth, Ellen P.

M.S.

May 2000

Forestry

Incorporating Competition Between Life Forms Into The Soil Water Submodel Within STAND-BGC, A Vegetative Process Model

Director: Kelsey Milner *K&M*

STAND-BGC is a mechanistic forest model at the stand level that grows grasses, shrubs, small trees and large trees. It uses standard forest inventory data as input and outputs an updated tree list. It has been found to perform well for well-established stands, but its behavior for stands where the understory is expected to have a large impact on the overstory (for example, for stands of small trees growing with high levels of grass cover) is less realistic. This study focused on modifying the modeling of belowground competition for soil moisture that takes place between life forms and size classes to improve the behavior of STAND-BGC for these situations. The water balance of the model was modified to reflect Walter's (1971) two-layer theory of resource partitioning. The behavior of the revised model was improved over the original version. As small trees developed into large trees, they were able to decouple their water use from grass competition, i.e., they grew out of the 'zone of competition'. The two-layer model produced seasonal patterns of soil moisture which were in accordance with Walter's two-layer hypothesis of resource partitioning.

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INCORPORATING COMPETITION BETWEEN LIFE FORMS INTO THE SOIL WATER SUBMODEL WITHIN STAND-BGC, A VEGETATIVE PROCESS MODEL

1. INTRODUCTION

The inland northwest region is characterized by relatively low annual precipitation (30 – 75 cm) with most of the moisture coming in the winter and spring, followed by a normal pattern of summer drought and some fall recharge. In this environment, survival and growth of young trees is strongly influenced by soil water availability. Under these conditions, grass can be a strong competitor with small trees for soil moisture. This has been shown in numerous studies which have demonstrated beneficial effects of site preparation and release treatments on the survival and early growth of trees due to the reduced competition from grass for soil water (Baron, 1962; Larson and Schubert, 1969; McDonald, 1986; Caldwell, Sucoff and Dixon, 1995; Kolb and Robberecht, 1996b) .

While the importance of tree/grass interactions is recognized in practice for establishing stands, the growth and yield models commonly used in the region do not incorporate non-tree vegetation interactions. Thus, they are of limited utility in simulating early stand growth. STAND-BGC (Milner and Coble, 1995) is a model which was developed to mechanistically simulate the simultaneous development of trees, shrubs and grasses and their interactions.

1.1 Description of STAND-BGC

STAND-BGC is a process-based, or mechanistic, model consisting of a series of submodels that describe the operation of various physiological processes involved in the growth of individual trees, shrubs and grasses. It is a member of a family of models using the canopy level modeling logic and physiological growth algorithms presented by Running and Coughlan in the FOREST-BGC (BioGeoChemical) model (1988) and the BIOME-BGC model (Running and Hunt, 1993). STAND-BGC takes the canopy level processes in the prior BGC models and applies them to multiple, interacting canopies thereby allowing simulation of the competitive interactions between vegetative life forms. This allows it to model both inter-specific competition between trees and grasses as well as intra-specific competition between trees of different life-stages. The basic processes within STAND-BGC are modeled at the individual 'entity' level (trees are grown as individual entities; grasses and shrubs are grown as unit-area entities). The processes modeled include: radiation interception by the foliage, carbon fixation by photosynthesis, carbon losses by respiration, the water balance of the stand, (including canopy interception, evaporation, transpiration, and drainage), the allocation of carbon to the component parts of the tree, mortality, and the updating of entity attributes (e.g., diameter, height and crown ratio).

STAND-BGC adapted the 'big-leaf' canopy level logic of the FOREST-BGC model to function at multiple sub-canopies, thus allowing more explicit representation of the competition for light and water between individual entities. Light competition between plant size classes and life forms is represented by the attenuation of light down through the canopy. Entities receive light energy based on their vertical position in the

stand and on the amount of leaf area they carry in their canopies. Larger (taller) entities capture light first, which is then subtracted from the light energy available to entities at lower canopy zones. Moisture competition is simulated in the model by assuming an entity has access to available soil water based on its leaf area proportional to the leaf area of the stand. This allows moisture competition to be modeled without defining rooting characteristics.

Physiological processes are modeled on a daily basis for each canopy zone of an entity and are more fully described in Milner and Coble (1995). In brief, they are calculated as follows: Daily photosynthesis in a specific canopy zone of an individual entity is calculated based on the maximum photosynthetic rate, photosynthetically active radiation, LAI, and a canopy light extinction coefficient. Daily canopy stomatal conductance to water vapor for each entity/canopy zone is calculated based on maximum stomatal conductance, attenuated radiation, and LAI (Milner and Coble 1995). Daily transpiration by entity/canopy zone is calculated from the Penmon-Monteith equation (Running and Coughlan 1988). Daily maintenance respiration for an entity is calculated using leaf, stem and root maintenance respiration constants, the average night temperature, the amount of carbon in leaf, stem or roots and daylength. Daily growth respiration for an entity is calculated as a fraction of gross photosynthesis.

STAND-BGC is a distance independent, individual entity (tree, shrub or grass) model, constructed to use standard forest inventory data as input, (for trees: species, diameter, height, crown ratio, and expansion factor; for shrubs and grasses: species, height and percent cover). These input data are converted to leaf carbon, stem carbon and root carbon units via biomass equations (biomass references cited in Milner and

Coble 1995). The model is driven by soil data (soil water holding capacity and soil texture) and climate data (daily precipitation, maximum and minimum air temperatures, relative humidity, dew point, and incident short-wave radiation) for the site, along with specified default generic conifer, shrub, and grass physiological parameters. See Appendix A for a table of required daily inputs, driving variables and outputs.

Ecophysiological attributes such as boundary layer conductance, specific leaf area, maximum stomatal conductance, leaf turnover rates, and respiration coefficients, can be modified to match the information available about a particular species or life form. The hydrologic, photosynthetic, and respiration processes are simulated on a daily timestep, while carbon allocation and mortality are simulated on an annual timestep. At the end of the growth period, net photosynthesis for the year is determined (net photosynthesis = gross photosynthesis – respiration), and is allocated between leaf, stem, and root carbon pools for each entity. After carbon is allocated to the entity carbon pools, the entity attributes are updated. For trees, the stem carbon allocation is first converted to biomass and then to volume through a set of unit conversions. Diameter increment is then calculated from the predicted stem volume increment, following Pressler's Law (as formulated by Mitchell, 1975). Height is updated by using the predicted diameter increment in the height growth equations used in FVS (Wykoff et al. 1982, p. 65 – 67). For shrubs and grasses, changes in percent cover and height are calculated by converting the carbon increment to biomass, inverting the appropriate biomass equations and solving the equation. The model produces a standard updated tree list with tree dimensions (DBH, height, crown ratio, density (tph), etc.) as output.

Mortality is simulated by STAND-BGC by removing an entity from the live entity list to be grown in the next growth period. If respiration costs exceed carbon production by photosynthesis, the leaf area of an entity is reduced. Crown recession for a tree occurs when the leaf carbon pool at the end of an annual growth period is less than the leaf carbon pool at the beginning of the growth period. In this case, the tree's crown ratio is reduced proportional to the loss of leaf carbon. When a tree's crown ratio is reduced to zero, the tree 'dies', i.e., it is removed from the live tree list and added to the dead tree list. For grasses, if carbon production is less than carbon lost to maintenance costs, the leaf carbon pool for the grass entity is reduced, resulting in a comparable decrease in height and percent cover. If percent crown cover is reduced to zero, the grass entity 'dies' and is removed from the live entity list.

1.2 Performance of STAND-BGC

For remeasured permanent plots in western Montana, Milner and Coble (1995) found that STAND-BGC predicted tree volume growth as well as or better than FVS (Forest Vegetation Simulator, nee Prognosis; Stage, 1973), a tree growth model commonly used in the northwest. However, the plots measured by Milner and Coble were located in well-established stands, where the understory likely had little influence on overstory growth. Subsequent investigations by Milner have indicated that the behavior of STAND-BGC for stands where the understory is expected to have a large impact on the overstory (for example, for stands of small trees growing with high levels of grass cover), is less realistic. STAND-BGC exhibited two unrealistic behaviors under those stand conditions: 1) Small trees experienced severe levels of mortality, even at low levels of grass cover. Those small trees that did survive, showed little, if any, evidence of

overcoming the competition of grass cover with time. 2) Increasing levels of grass cover unduly suppressed the growth of large trees.

While competition for light resources in the model takes place between entities based on their canopy size and vertical position, competition for soil moisture is based solely on the above-ground leaf area of the entities. This simplification was based on the theory that the more leaf area a plant has, the more roots it can support, thus the more soil area the plant can access, and the more water it can obtain. However, differential distribution of roots within the soil profile by different plant life forms and size classes may result in resource partitioning which could highly affect the interactions of the vegetation on the site. This concept is not taken into account by the original soil water submodel in STAND-BGC. This omission limits application of the model as a management tool for early stand development and as a simulator for development of stands where non-tree vegetation is a major competitor for light, nutrients and water (e.g., in young plantations). Adding a level of realism to the functional relationships within the soil water submodel should improve the behavior of the model.

2. OBJECTIVE

The more closely process models can be made to represent true functional relationships, the more reliable their predictions will become. The objective of this study was twofold:

- 1) To revise the original single-layer soil water submodel within STAND-BGC to a two-layer soil water submodel which simulated the resource partitioning of soil water by different plant life forms and size classes as reported in current literature.

2) To examine the behavior of the revised STAND-BGC model for small and large trees grown under varying levels of grass cover. I.e., does the revised model result in reasonable patterns of mortality and in valid LAI, height and diameter values.

Revising the modeling of water competition in STAND-BGC should improve the behavior of the model to more realistically simulate growth of complex forest structures by modeling the development and competitive interactions of all vegetation on the stand.

3. LITERATURE REVIEW

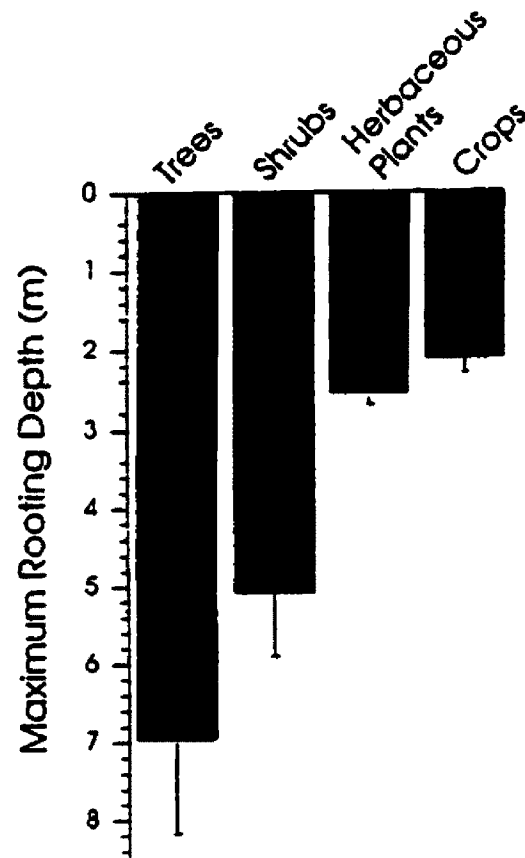
Competitive interactions fall into two main categories: aboveground competition for energy, i.e., light, and belowground competition for water and nutrients. This study focused on improving the modeling of belowground competition for soil moisture that takes place between life forms and size classes. In water-limited ecosystems, grass and seedling competition studies (Pearson 1934; Baron 1962; Larson and Schubert 1969; Harrington and Kelsey 1979; Sands and Nambiar 1983; Shainsky and Radosevich 1986; McDonald 1986; Caldwell, et al. 1995; Kolb and Robberecht 1996b) have shown that interactions between life forms (e.g., grasses and woody plants) can have a large impact on the establishment and early development of forest stands.

3.1 Interspecific Resource Partitioning

In a review of 290 observations of rooting depth which covered 255 different plant species from 11 biomes, Canadell, et al. (1996) found that when grouping all the species across biomes by three basic functional groups, trees, shrubs and herbaceous

plants, the mean reported maximum rooting depths were significantly different (Figure 1).

FIGURE 1.
290 observations of rooting
depth covering 255 different
plant species from 11 biomes
grouped by basic functional
groups. Mean and SE of
reported maximum rooting
depth (m) by three major
functional groups (trees,
shrubs, and herbaceous
plants) and crops.
From Canadell, et al. 1996



Several studies have shown that plants with different rooting habits show different seasonal patterns of water potential (Davis and Mooney 1986; Crombie et al. 1988; Sala et al. 1989; Hodgkinson 1992). Those plants that appear to be shallow rooted exhibit the lowest water potentials (most stress) and the lowest leaf conductances. They also respond first to a new input of soil moisture. Those plants that presumably get water from considerable depths, still have relatively high water potentials (less negative) and high leaf conductance values throughout the summer drought season – indicating a stable

water source corresponding to a consistent pattern of soil moisture availability at lower depths.

Such water resource partitioning between plant life forms (i.e., grasses and woody plants) has been reported in South African savannas (Knoop and Walker 1985), the Patagonian steppe (Soriano and Sala 1983; Sala et al. 1989; Schulze et al. 1996), central semi-arid Argentina (Pelaez et al. 1994), a Kenyan savanna (Hesla et al. 1985), and a North American subtropical thorn woodland (Brown and Archer 1990).

Isotopic studies can be used to trace where, when and how, different co-occurring (and potentially competing) plant species access the water resources currently available in a particular habitat. For example, Ehleringer et al. (1991) demonstrated that certain desert species within the same community use shallow soil water, others use soil moisture from deep soil layers and still others use some combination of these two sources. In the seasonally wet tropics, Jackson et al. (1995) have recorded that evergreen and deciduous tree species use deeper and more shallow water sources, respectively.

3.2 Intraspecific Resource Partitioning

Soil water resource partitioning has also been identified intraspecifically between different life-history classes (seedlings vs. adult: Brown and Archer, 1990; Frazer and Davis, 1988; Donovan and Ehleringer, 1991 and 1992) and size classes (small vs. large: Donovan and Ehleringer, 1992, 1994; Dawson 1996) for woody plants. Frazer and Davis (1988) found differences between the water potentials of seedling and adult plants as a function of rooting depth and soil moisture. Donovan and Ehleringer (1991) showed that juvenile plants differed from mature plants in several ecophysiological characteristics, including water potential, stomatal conductance, photosynthetic rate and

water-use efficiency. In general, smaller plants are more water stressed than larger adults. This has been attributed to differences in rooting depth and soil moisture availability. Lower xylem pressure potentials (higher water stress) are generally accompanied by lower rates of photosynthesis and conductance.

Donovan and Ehleringer (1992) investigated ecophysiological characteristics of plants from different size and life-history classes in a field population of *Chrysothamnus nauseosus*. They found that:

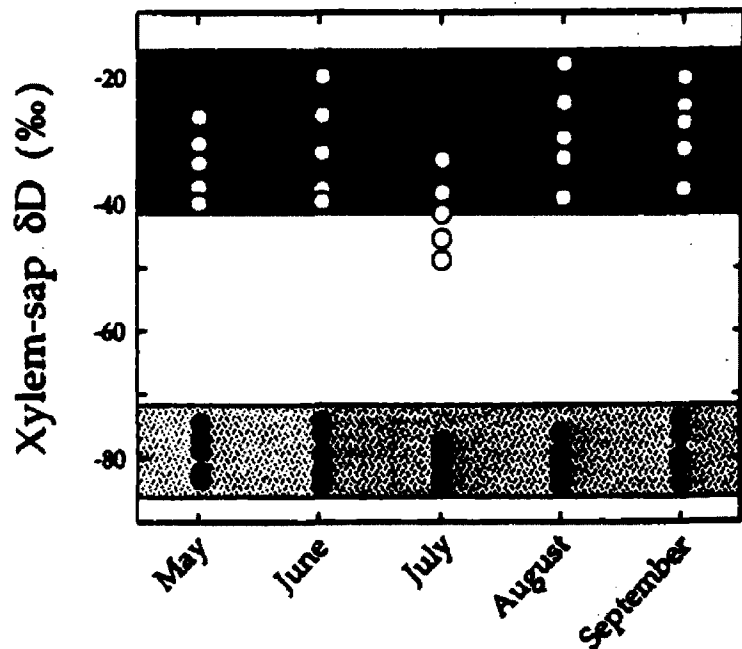
- Juvenile plants had higher rates of photosynthesis, stomatal conductance and transpiration than reproductive adults, even though pre-dawn xylem pressure potentials of juveniles were slightly lower. Juveniles were also less water-use efficient.
- A comparison of carbon isotope discrimination values (Δ) indicated a gradient of water-use efficiency that was correlated with size:
Seedlings < Juveniles = Small Adults < Large Adults
- Small establishing plants may experience short-term environmental conditions and long-term selective pressures different from those of larger reproductive plants.
- The pattern of smaller plants having higher rate of gas exchange and less efficient use of water in the absence of higher pre-dawn xylem pressure potentials suggest a developmental progression in ecophysiological parameters with increasing size.

Kolb and Robberecht studied Ponderosa pine seedling survival and water use and observed similar changes as trees develop (1996a). They concluded that Ponderosa pine seedlings experienced transpiration rates that were much higher than those at later stages in their life-history and that their early survival on hot dry sites depended primarily on their capacity for heat dissipation through this rapid transpiration while in the seedling stage.

Based on isotopic analysis, Dawson (1996) found that large trees and forest stands composed of trees greater than 10 meters tall transpired only ground water from deep soil layers, whereas small trees and forest stands composed of younger trees almost exclusively used soil water from the upper soil layers (Figure 2). He also demonstrated

that the water source used by a tree species influences its water use patterns. For example, small trees showed greater variation in transpiration rates than large trees reflecting their access only to soil water, which is more susceptible to large oscillations in water potential than groundwater.

FIGURE 2. As plants get bigger, they draw their water from different sources. The stable hydrogen isotope composition (δD) of water extracted from the xylem sap of small (○) and large (●) trees. The dark band across the top is soil water values. The stippled band across the bottom is groundwater values.
From Dawson 1996



Weltzin and McPherson (1997) showed that *Quercus emoryi* trees used different source water at different developmental stages. They distinguished three functional groups intraspecifically: very young tree seedlings used water from shallower depths in the profile than grasses and older seedlings -- which may enhance germination and early establishment. 1 and 2-yr old seedlings competed directly with the grass for soil water, whereas saplings and mature trees accessed soil water from deeper in the soil profile than did grasses and either group of seedlings.

In Australia, Dawson and Pate (1996) showed that woody plant species with dimorphic root systems could alter the way they pulled water from the soil. As the soil

profile dried from the top down, *B. prionotes* and the other species they examined appeared to draw proportionally more water from deeper in the soil profile via sinker roots. In accordance with this, White, et al. (1985) showed that white pine trees in the eastern United States switched from surface soil moisture to deeper layers for their water extraction depending on the recent history of precipitation events.

As plants develop they may show different patterns of water acquisition. Initially, seedlings and grasses compete directly for the same soil resources. Because grass roots are very dense in the upper layers and because they have high conductances, grass water uptake can preempt site resources to the point that seedlings either experience difficulty becoming established or, once established, still can't grow at the potential of the site. As tree roots grow and access deeper water sources, they effectively grow out of this 'zone of competition' from grass roots, with a resultant partitioning of soil moisture. This partitioning of soil moisture is elegantly described by Walter's (1971) two-layer model which incorporates many of the details revealed by other studies.

3.3 Two-Layer Model Of Soil Water Resource Partitioning

Walter (1971) described a two-layer model of soil water resource partitioning for a savanna ecosystem. He depicted grasses and woody plants as 'antagonistic plant types' (or functional life forms) differing in their root systems and water use patterns. Grasses will be shallow-rooted, having most of their dense, fibrous roots in the upper soil layer, and will thus be limited in their ability to exploit deep soil resources. Because they are rooted in the surface layers, they will depend primarily on growing season precipitation which is quite variable. Woody plants, because of their characteristic rooting patterns (less dense, not fibrous, but with a strong taproot) will be less efficient than grasses at

exploiting resources in the upper soil layers but capable of exploiting resources stored deep in the soil. They will depend mainly on winter precipitation that percolates through surface soil layers when grasses are dormant and on large rain events that also escape grass capture.

A model such as Walter's assumes that woody plant roots (as successful regeneration) can tolerate the presence of grass roots long enough to penetrate beyond their influence. As woody plant seedling roots reach greater depths in the soil profile, they would be less vulnerable to belowground interference from grass roots which only colonize upper soil layers. Initially, seedlings and grasses compete directly for the same soil resources. As tree roots grow and access deeper water sources, they effectively grow out of the zone of competition with grass roots, resulting in a partitioning of soil moisture.

Spatial and temporal partitioning of soil resources are often related. The different life forms have also developed differential timing of growth to take advantage of different patterns of water availability in the part of the soil profile that they access. Deep roots may allow plants access to another water source available after upper soil layers have dried out, enabling them to decouple the timing of growth from rainfall events, thus persisting after neighboring species have died or become dormant. Grasses, which rely on growing season precipitation, complete their life cycle quickly and go dormant. They tend to be profligate water users, keeping their stomates open even at low water potentials. They can continue to transpire at lower water potentials (higher water stress) than do woody plants. Trees can take advantage of the beginning and end of the growing season when grasses are dormant. Their reliance on the more consistent water source

from deeper layers allows them to be conservative in their water use, shutting down their stomates at higher water potentials (lower water stress) while still obtaining enough moisture to complete their life cycle successfully.

4. METHODS

4.1 Approach

It is the contention of growth modelers, that once competition for light has been taken adequately into account, belowground resource partitioning becomes the most important mechanism to describing interactions within complex forest stand structures (particularly in water-limited ecosystems). It would be daunting to estimate all the necessary parameters for this submodel at the species level (rooting densities, rooting profiles and active extraction zones, etc. for each species). A balance needs to be struck between increasing the complexity of models to capture important interactions and maintaining simplicity to keep the data collection needs attainable.

In order to achieve this balance a distinction is made between life forms (grasses, shrubs, and trees) and between size classes of woody plants (small vs. large) based on their differential access to soil resources (i.e., rooting depths). Implementing Walter's two-layer theory of resource partitioning and describing the water balance in terms of functional groups and size classes adds at least one more level of reality to the model without requiring a large increase in input data. To this purpose, the water balance submodel within STAND-BGC was revised from a single soil layer process to a two-layer soil water process allowing differential access by entities to soil water based on their size.

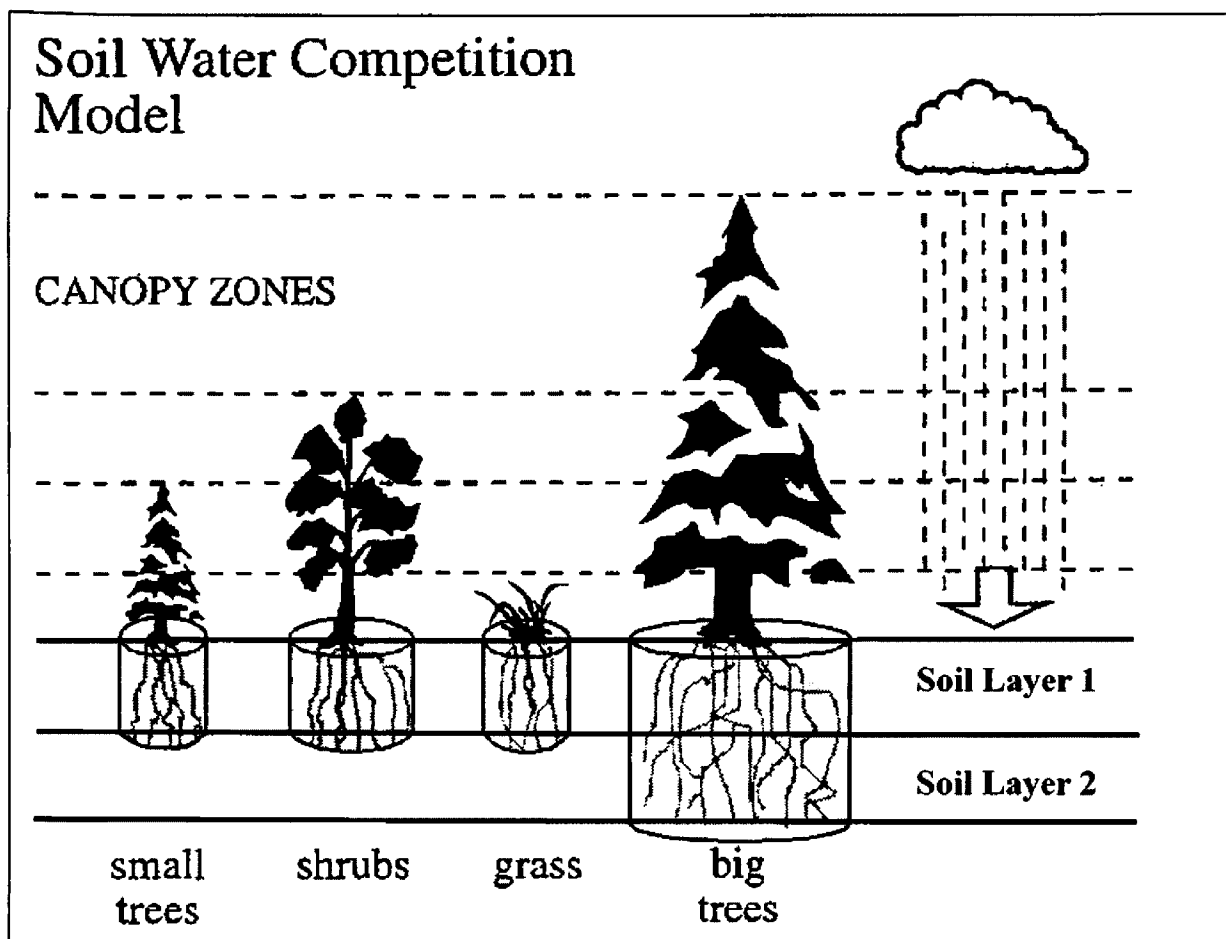


FIGURE 3. Simple schematic of two-layer soil submodel showing differential access to soil water by entities.

4.2 Logic of two-layer soil water model within STAND-BGC

The original version of STAND-BGC used a single soil layer model to describe water balance. No resource partitioning for subsoil moisture between life forms or size classes was included. The modified water balance operates at two levels, the site level and the individual plant or entity level. Trees experience differential access to the two soil layers based on their height (see Figure 3). *Small* trees are defined as trees less than 1.3 meters (4.5 feet) in height. *Large* trees are those 1.3 meters or greater in height. This

cutoff point assumes a symmetrical development of the root system with the above-ground development. This height reflects the ‘rule-of-thumb’ often used in field forestry that trees this size or above are generally considered to be ‘free to grow’, that is, they have escaped the influence of grass competition by this point. This size of trees is thought to have started growing out of the zone of competition with grasses because their root system is developed enough to start accessing water stored in deeper soil layers which grass roots cannot reach. However, it must be kept in mind that this transition point is not well defined and that trees may never completely escape competition from grass – particularly for the nutrients in the upper soil layers. Gaining access to deeper soil layers is in all probability not a sudden event. Rather, it is more likely a gradual transition – as roots grow deeper, they gradually have more access to lower soil layers which are out of reach of the maximum extension of grass roots. However, for exploring growth model behavior incorporating soil water partitioning this is an adequate first approach.

4.2.1 Site level water balance

At the site level (A in Figure 4), daily precipitation is distributed into two soil layers depending on their soil water holding capacities (m^3/m^3). Each soil layer contains stored water, referred to as the soil water content (item A1 in Figure 4: SWC is in m^3/ha), to which water is added by precipitation, and from which water is lost by transpiration, evaporation and drainage to deeper soil layers. Snowmelt is distributed equally between the two soil layers. This is based on the presumption that in early spring when snow is melting, the two soil layers are both fully recharged and come to equilibrium due to the

large availability of water, low evaporation rates, and low transpiration rates experienced at that time of year. Rain events only enter the top layer (minus canopy interception). If it is a large rain event, and the top layer's soil water holding capacity is exceeded, 'outflow' from soil layer 1 enters soil layer 2. Outflow from soil layer 2 is lost (to plants) to groundwater or deep drainage. Soil water potentials (item A2 in Figure 4: SWP is in MPa) for each layer are calculated based on the soil water content of that layer. Evaporation is calculated and subtracted only from the top layer. The sum of daily transpiration from *grass* and *small* trees is also subtracted only from the top layer only (item A3 in Figure 4). Following the patterns found by White, et al. (1985) and Dawson and Pate (1996), (showed that large trees could switch their water extraction between deep and surface soil layers based on the recent history of precipitation events) the sum of daily transpiration of all *large* trees is subtracted from whichever soil layer currently is experiencing the least water stress (i.e., the highest water potential) (item A4 in Figure 4).

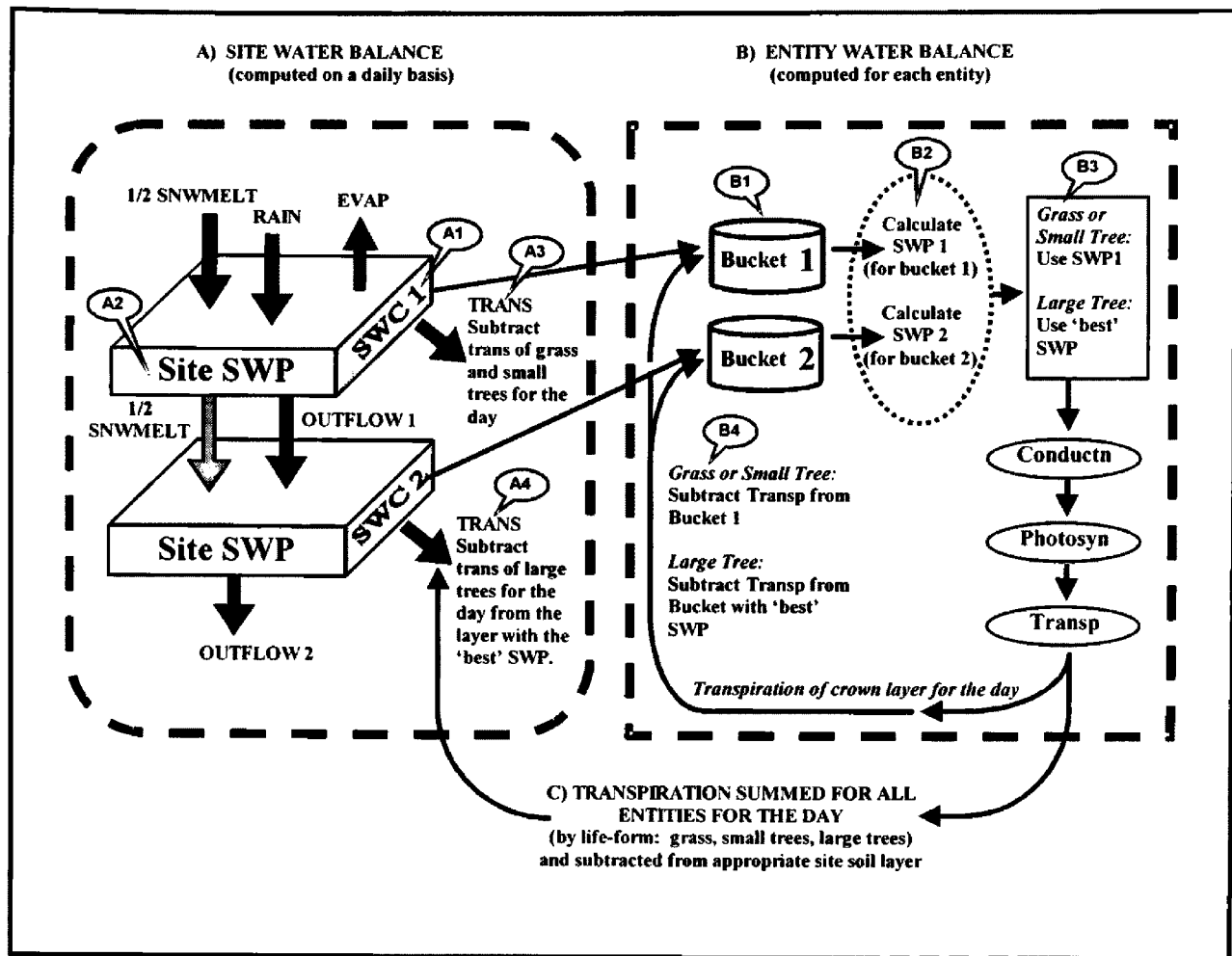


FIGURE 4. Site Water Balance for two-layer soil water model in STAND-BGC. See text for explanation and description.

4.2.2 Entity level water balance

The moisture competition submodel allows entities (trees, shrubs or grasses) access to site water (B in Figure 4) based upon the amount of leaf area in an entity relative to the total leaf area on the site. First, the portion of leaf area on the site allocated to each entity is calculated as:

$$\text{RATIO} = \text{LA}_{\text{entity}} / \text{LA}_{\text{site}}$$

Then, the area accessed for soil water by the entity (its 'occupancy') is computed as:

$$\text{OCPNCY} = \text{RATIO} * \text{AREA}$$

where AREA = ground area = 10,000 m². So, as the total leaf area increases or decreases or if the leaf area of an entity changes, RATIO also changes and the amount of soil accessed changes. The amount of site water available to an entity (which we will refer to as the entity's 'water bucket') is calculated for each entity. A separate water bucket is calculated for each soil layer (item B1 in Figure 4) based on RATIO and on the soil water content (SWC) of the two site soil layers (A1 in Figure 4). Soil water potential for each bucket (item B2 in Figure 4) is then calculated from OCPNCY, soil depth, soil texture and soil water content of the respective soil layer. Conductance, transpiration and photosynthesis of *grasses* and *small* trees are calculated by canopy zone using the soil water potential of the top bucket, whereas these processes for *large* trees are based on the 'best', i.e., least negative, soil water potential (item B3 in Figure 4). Water is drawn down by transpiration from the bucket upon which the calculation was based (item B4 in Figure 4). Water depletion of an entity's bucket does not affect water potentials in other buckets on a daily basis. The transpiration of all entities for the day is summed by life form to feed back into the total site water available per soil layer (C in Figure 4). Each bucket is assumed to equilibrate to the site water potential of its corresponding soil layer at the start of the following day. The two soil layers, may, (and in fact, are expected to) show different soil water potentials throughout the season.

4.3 Simulations

The climate and soil inputs of STAND-BGC were approximated to simulate a site on a south-facing slope in the Potomac valley of western Montana. Soil depth, texture coefficients, and other model parameters were either obtainable for this area or set to approximate this location. A climate file from an established weather station in this area

was obtained and used for the climate inputs (daily solar insolation, maximum and minimum temperatures, relative humidity and precipitation). Three levels of grass cover – none, low, and high, were simulated for each type of stand structure modeled. In preliminary model simulations with only grass on the site, the maximum leaf area index (LAI, projected leaf area per unit of ground area) the site was able to maintain was 0.35 m²/m². Since this LAI value is within the range of values presented in Table 1 for a variety of grass communities, it appears to be a realistic one, particularly for the more arid communities. This value translates to a grass cover of approximately 40%. This was chosen as the ‘high’ simulated level of grass cover. All input files consisted of 22 tree records representing a 1/50th hectare ‘plot’, so each tree record was multiplied by 50 (expansion factor = 50) to calculate the values on a per hectare basis, resulting in 1100 tph. All model simulations were for a 30-year time period.

Table 1. A sample of Leaf Area Indexes (LAIs) of grass communities taken from several studies.

Type of community	LAI (m ² m ⁻²)	Source
Panicum <i>maximum</i> stand in Cuban savanna	0.68 – 3.27	Suarez et al, 1989
Festuca Grassland in Patagonia	1.0	Schulze, et al, 1996
Stipa Grassland in Patagonia	0.4	
Shortgrass steppe communities in Colorado	0.31 – 0.55	Hazlett,1992
Chihuahuan Desert grass communities	0.1 – 0.2	Gibbins, et al., 1996

Three forest stand structures were simulated to evaluate STAND-BGC model behavior. The first set of simulations represented a stand of *small* trees growing in competition with varying levels of grass cover. This situation would commonly be found

in naturally regenerated forest stands that are in the early initiation stage (Oliver, 1990) and in plantations which have been recently established. The input file for this stand consisted of 22 records representing 1100 trees per hectare (tph) ranging in height from 0.3 meters to 0.6 meters and with basal diameters ranging from 1.2 to 2.8 cm. The second set of projections simulated a stand of *large* trees, also growing with varying levels of grass competition. Density was again set to 1100 tph. Heights ranged from 2.0 to 4.5 meters (all greater than the cutoff point of 1.3 meters discussed earlier as the transition point from small to large trees) and diameters from 5.0 to 10.0 cm. This type of forest stand would occur in the same situations as the *small* stand, but is slightly advanced in age and size. The third set of simulations represented a mixed size class forest structure. The input file consisted of 400 tph *small* trees (0.2 to 1.2 meters) and 750 tph *large* trees (1.8 to 21.2 meters in height) for a total density of 1150 tph, again grown with varying levels of grass cover. The tree data in this *mixed* input file were taken from an actual sample plot installed in the same area where the climate file and soil data originated (i.e., the Potomac valley of western Montana).

Model behavior was evaluated over a 30-year period by examining trends in stand development, particularly the interactions between grass and trees. Behavior of the two-layer soil water submodel was compared to the behavior of the original STAND-BGC model using the single-layer soil water submodel to judge if it more accurately simulated competition between life forms. Behavior of the growth model was also evaluated by examining seasonal patterns of soil water potentials for the two simulated soil layers in the two-layer submodel and comparing the simulated patterns to expected soil moisture patterns as concluded from the literature.

5. SIMULATION RESULTS AND MODEL BEHAVIOR

To compare the behavior of the new version of STAND-BGC (with the two-layer soil water submodel) to the behavior of the original, single-layer version, the hypothetical stand of small trees was simulated with varying levels of grass cover by both models. For no grass cover, the two models estimated similar leaf area indexes for a 30-year time period (Figure 5a and 5d). Neither model version produced any tree mortality within that time period and the height and diameter structures of the plots were comparable (Figures 6a and 7a).

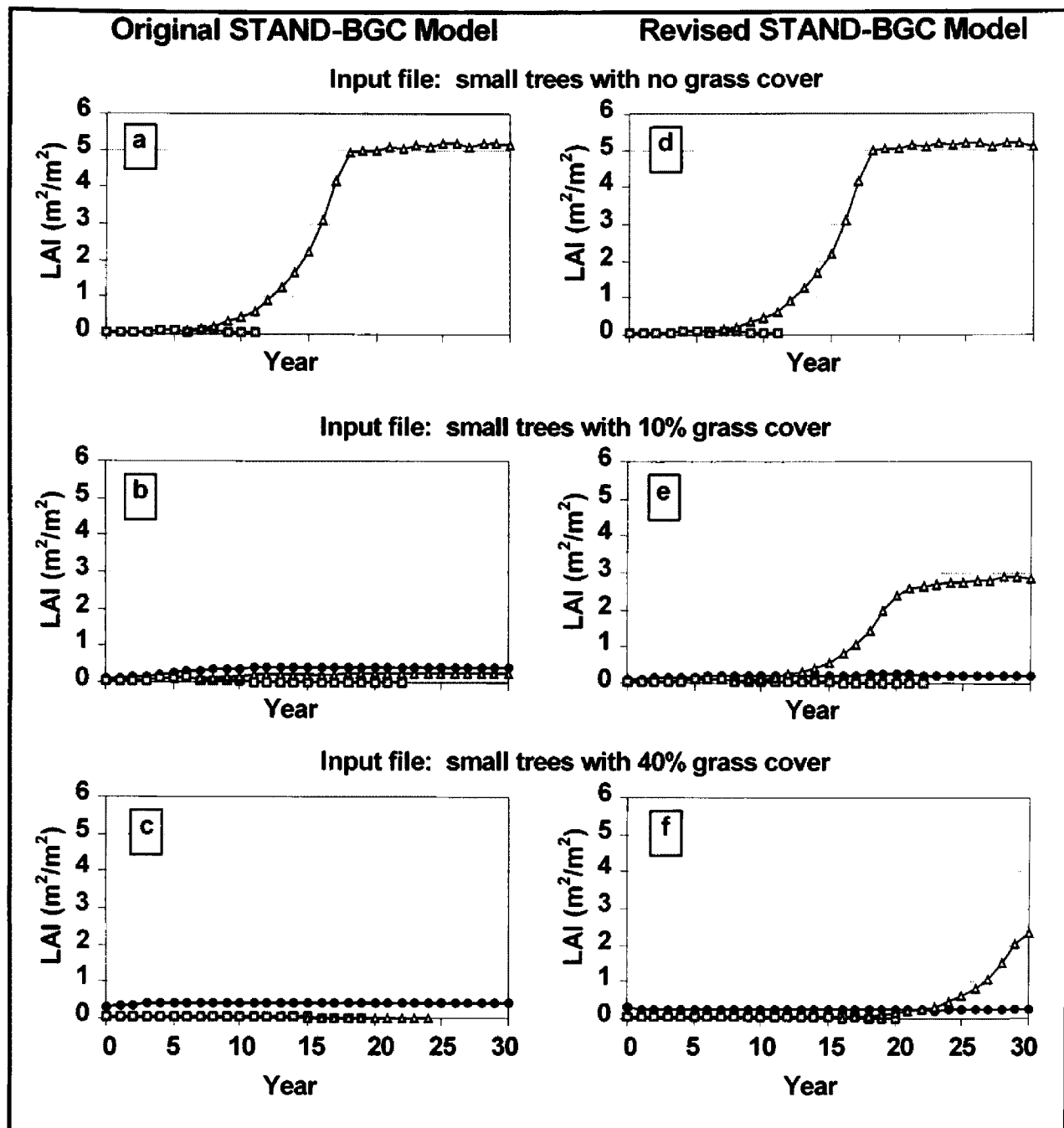


FIGURE 5. Predicted Leaf Area Index (LAI) under three levels of grass cover comparing the original and revised versions of STAND-BGC. LAI is plotted by year for life forms (grass, small trees, and large trees). Input files for model runs were small tree file with no grass cover (a, d) 10% grass cover (b, e) and 40% cover (c, f). The small tree component is affected by both mortality and growth. For example, in a and d, small trees experience no mortality, yet the small tree component disappears by year 12 as all small trees grow to be large trees. In c and f, the small tree component disappears by year 20. This is due to some small trees dying, starting in year 10, while others survive and grow enough to become large trees. In c, the large trees all die, leaving only grass on the site at the end of a 30-year projection.

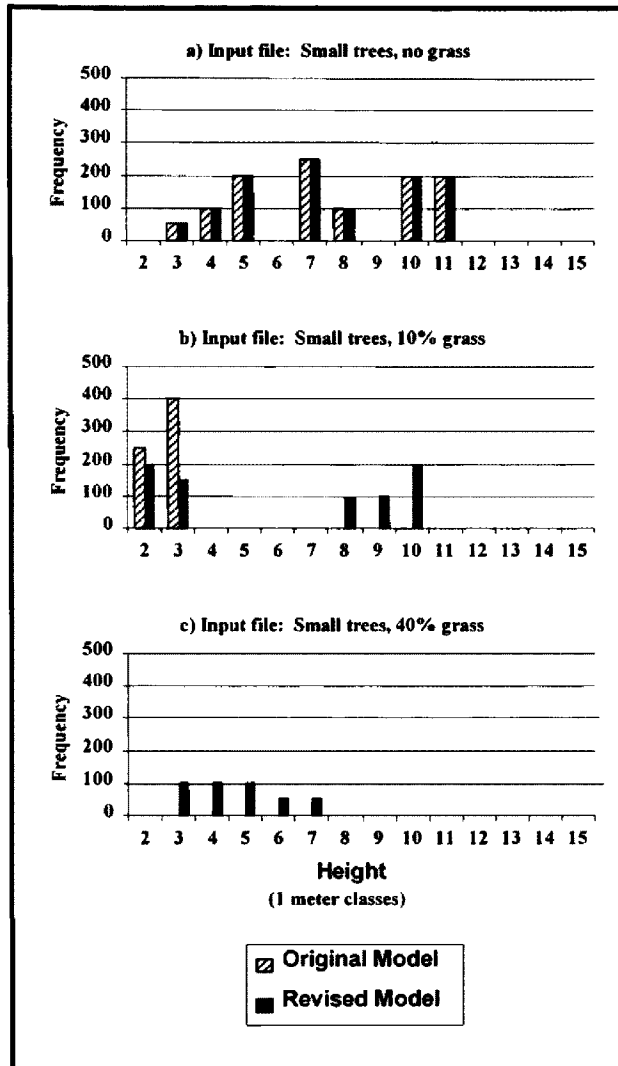


FIGURE 6. Height class distribution at end of 30-year projection for three levels of grass cover (0%, 10% and 40%). Input file for simulated stand consisted of small trees (0.3 m to 0.5 m) at a density of 1100 tph. Original model compared to revised model.

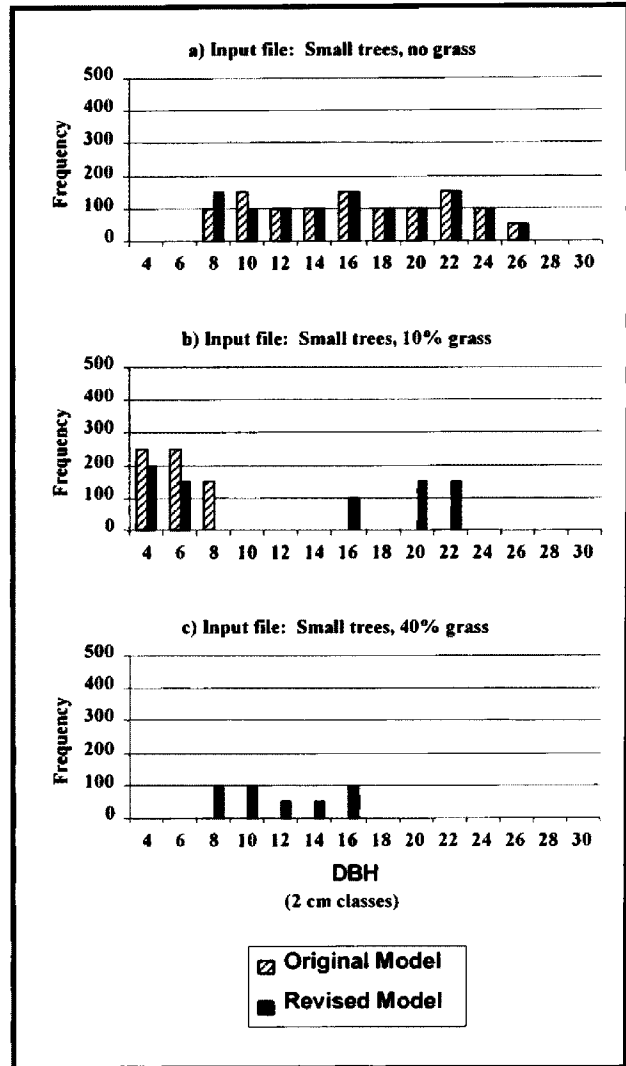


FIGURE 7. DBH class distribution at end of 30-year projection for three levels of grass cover (0%, 10% and 40%). Input file for simulated stand consisted of small trees (< 1.3 m in height) at a density of 1100 tph. Original model compared to revised model.

Introducing grass onto the site resulted in large differences in model behavior between the two model versions. Table 2 summarizes the mortality results from both models for two levels of grass cover for the small tree simulations.

Table 2. MORTALITY. Tree height at death versus year of death for the original and revised versions of STAND-BGC under two levels of grass cover.

Year Trees 'Died'	Tree Height (m) at Death			
	Original Model		Revised Model	
	10 % grass cover	40 % grass cover	10 % grass cover	40 % grass cover
10		0.54		0.50
11		0.56 0.57		0.51
12		0.58 0.59 0.60		0.54 0.55
13		0.61		0.57
14				0.58
15		0.86 0.86		
16		0.88 0.90		
17		0.92	0.74	
18	0.97	0.94	0.79	0.83 0.83
19	1.01	0.95		
20	1.04	1.26		0.89
21	1.07	1.26 1.28	0.83	
22	1.11	1.31	0.89	0.93
23		1.33	0.94	
24	1.14	1.36	0.99	0.97
25	1.18	1.39	1.03	
27		1.42		1.02
29	1.71 1.71			
30	1.77			
Number Dead (per hectare)	500	1100 (all)	350	700

The higher level of grass cover (40%) produced more mortality than the 10% level of grass cover for both models. Mortality also occurred earlier at the higher level of grass cover for both models. The total number of trees that died was lower for the revised model than for the original model, for both levels of grass cover, with no trees surviving to the end of the 30-year projection period for the original version simulation with 40% grass cover. The heights of the trees at time of death indicate that the original single-layer model not only killed more trees, but also killed larger (taller) trees than did the revised two-layer model.

The revised model displayed reduced suppression of tree growth as levels of grass increased on the site than did the original model. Tree LAIs of the revised simulation with grass on the site were lower than when there was no grass cover, but higher than the original model runs for both 10% and 40% grass cover (Figure 5). Furthermore, across all levels of grass cover the revised model displayed a point where there was a sharp increase in the LAI of large trees (although this transition point was delayed in time as grass cover levels increased). This pattern was not seen in the original model projection with grass cover present. Rather, even at 10% grass cover, the original model produced trees that never exceeded an LAI of $0.25 \text{ m}^2 \text{ m}^{-2}$, even though all the surviving trees were taller than 1.3m (large trees by our earlier definition). Figures 6 and 7 show height and DBH frequency distributions for a set of small trees over a 30-year projection under three levels of grass cover. Table 3 contains the average heights and DBHs at the end of the 30-year projection. Results from the revised model projection with 10% grass cover showed that out of an original 1100 tph, there were 750 survivors per hectare, with an average height of 6.05 m and an average DBH of 12.84 cm. In contrast, the original

model had only 650 survivors with an average height of 2.39 m and an average DBH of 5.12 cm. Results from the revised model projection with 40% grass cover yielded 400 survivors per hectare with an average height of 4.78 m and an average DBH of 12.11 cm compared to no survivors for the original model projection.

Table 3. Number survivors, average height and average DBH of small tree stand at end of 30-year projection under two levels of grass cover for original and revised versions of STAND-BGC.

Grass Cover	Original Model			Revised Model		
	# Trees Surviving (tph)	Height (m)	DBH (cm)	# Trees Surviving (tph)	Height (m)	DBH (cm)
10%	650	5.12	2.39	750	12.84	6.05
40%	no survivors	-	-	400	12.11	4.78

The two model versions also showed differences in LAI, heights and diameters for the simulated stand of large trees under varying levels of grass cover, although not as extreme as with the stand of small trees simulations. No grass cover with large trees resulted in final LAIs of 4.7 and 4.6 m²m⁻² for the original model and the revised model, respectively (Figure 8). Higher levels of grass (40 %) changed these values to 1.6 and 3.0 respectively (Figure 8). Height and diameter distributions for the large tree projections are presented in Figures 9 and 10. Increased leaf area associated with the revised model projections in Figure 8 result in larger heights and an even larger diameters. Average height and diameter distributions are presented in Table 4.

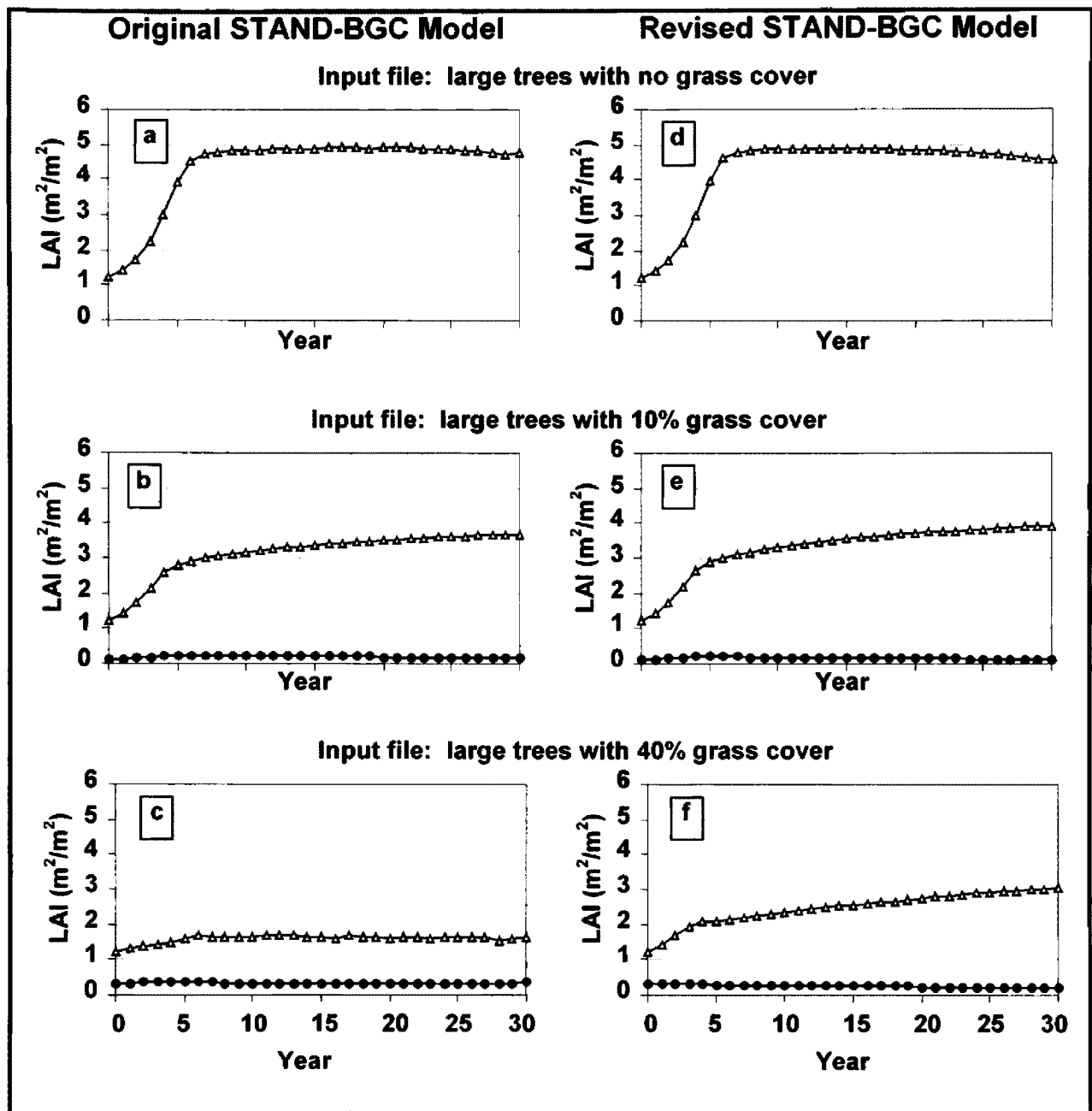


FIGURE 8. Predicted Leaf Area Index (LAI) of original, single-layer soil water model (a, b, c) compared to LAI of revised, two-layer model (d, e, f). LAI is plotted by year for life forms (grass, small trees, and large trees). Input files for model runs were large tree file with no grass cover (a, d) 10% grass cover (b, e) and 40% cover (c, f).

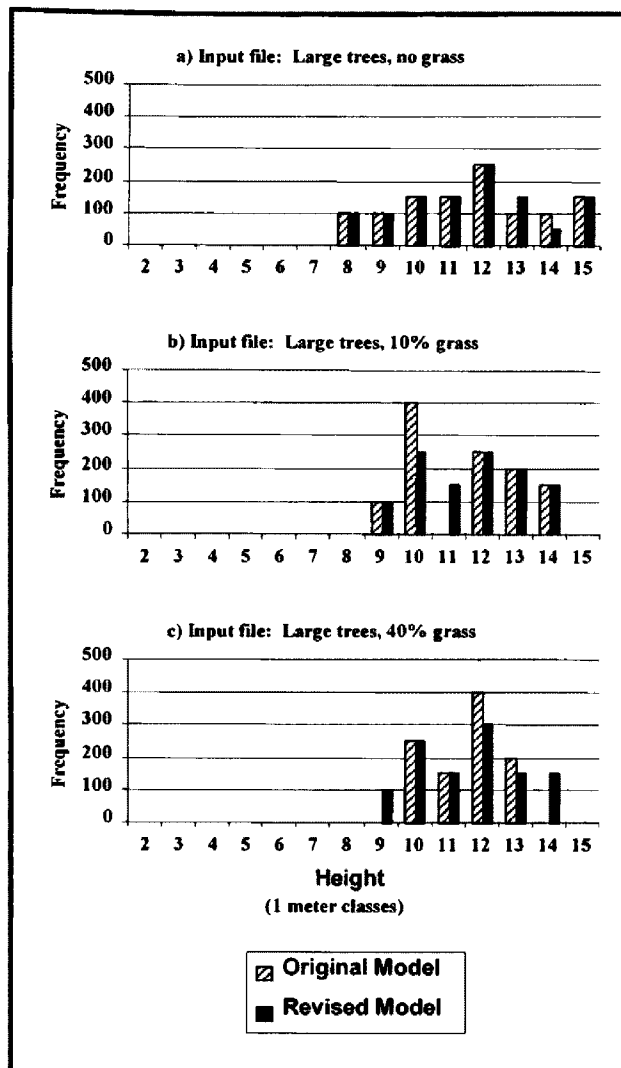


FIGURE 9. Height class distribution at end of 30-year projection under three levels of grass cover (0%, 10% and 40%). Initial stand components consisted of large trees (2.0 m to 5.0 m) at a density of 1100 tph. Original model compared to revised model.

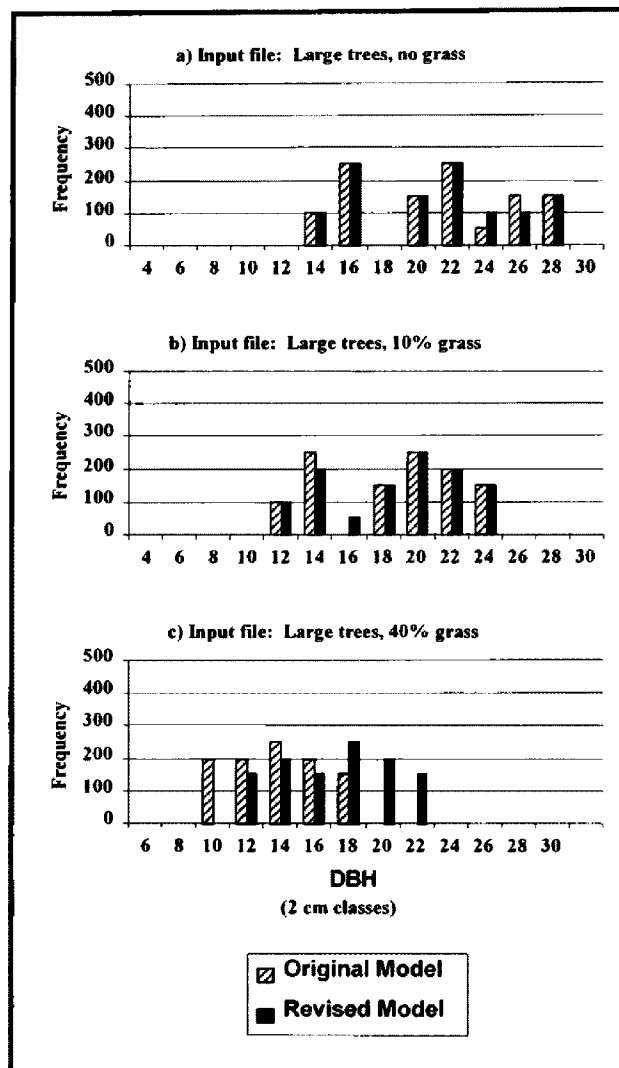


FIGURE 10. DBH class distribution at end of 30-year projection under three levels of grass cover (0%, 10% and 40%). Initial stand components consisted of large trees (2.0 m to 5.0 m in height) at a density of 1100 tph. Original model compared to revised model.

Table 4. Average height and DBH of large tree stand at end of 30-year projection for original and revised versions of STAND-BGC.

Grass Cover	Original Model		Revised Model	
	Height (m)	DBH (cm)	Height (m)	DBH (cm)
10%	11.37	18.64	11.45	19.10
40%	11.74	14.35	11.39	16.89

The mixed forest structure simulations showed little difference in LAI (Figure 11), height structure (Figure 12), diameter structure (Figure 13) or mortality between the two model versions or between differing levels of grass competition.

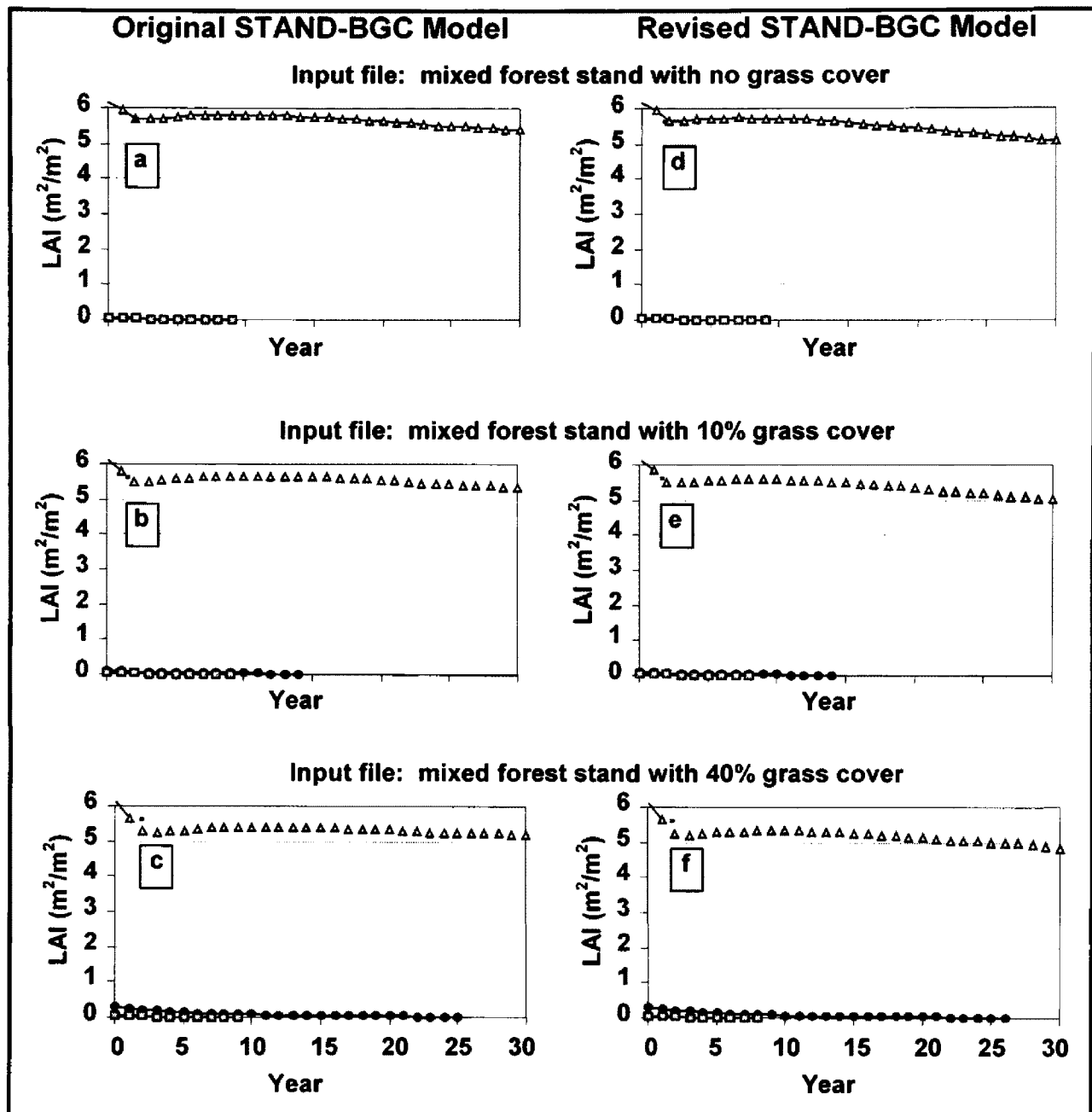
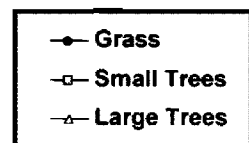


FIGURE 11. Predicted Leaf Area Index (LAI) of original, single-layer soil water model (a, b, c) compared to LAI of revised, two-layer model (d, e, f). LAI is plotted by year for life forms (grass, small trees, and large trees). Input files for model runs were small tree file with no grass cover (a, d) 10% grass cover (b, e) and 40% cover (c, f). The small tree component is affected by both mortality and growth.



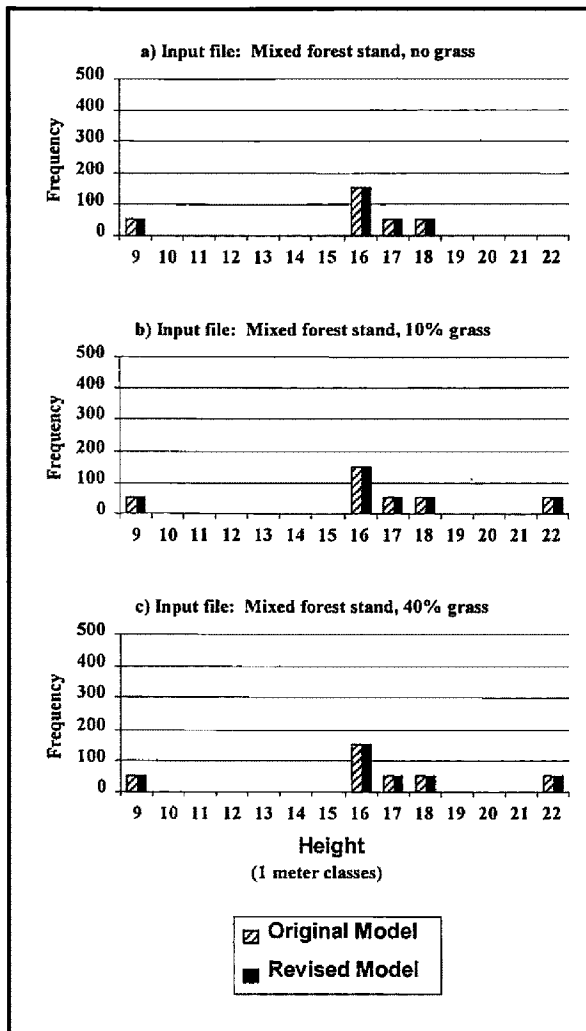


FIGURE 12. Height class distribution at end of 30-year run for three levels of grass cover (0%, 10% and 40%). Initial simulated stand consisted of a mix of small and large trees at a density of 1100 tph. Original model compared to revised model.

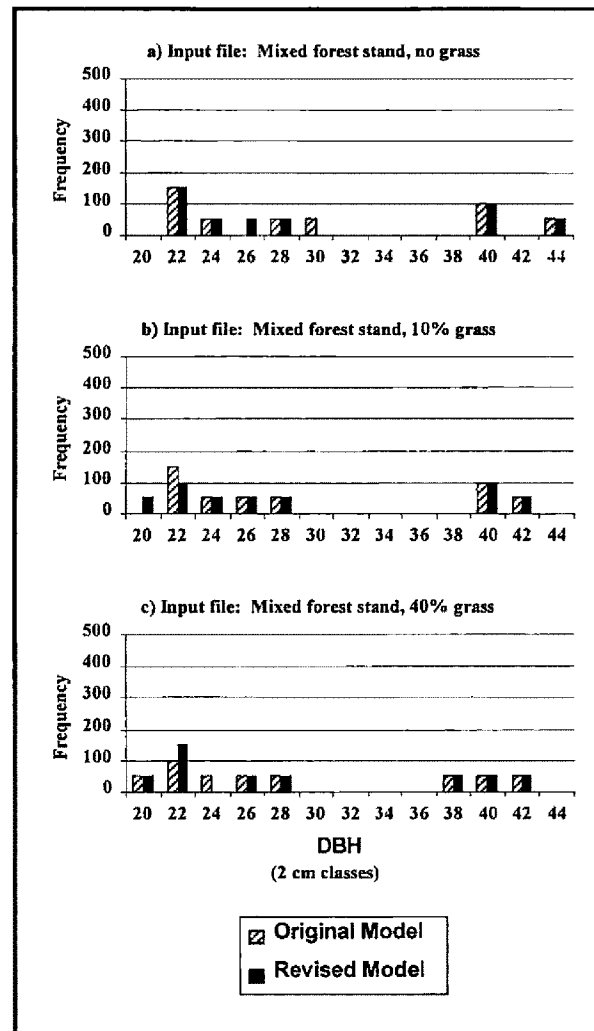


FIGURE 13. DBH class distribution at end of 30-year run for three levels of grass cover (0%, 10% and 40%). Initial simulated stand consisted of mixed small and large trees at a density of 1100 tph. Original model compared to revised model.

All of the small trees (400 tph) and the same number of larger trees (300 tph) died in both versions, even for simulations with no grass competition. The minimum soil water potential attained in the top layer (upon which small trees are solely dependent) was -2.35 MPa for the simulation of a mixed forest structure with 40% grass cover. This value was

less extreme than those reached by the top layer in earlier simulations where small trees survived to grow into large trees (e.g, the small trees with 40% grass cover projection – see SWPs in Figure 14). Since different levels of water stress did not result in differences in mortality, the recorded mortality was probably due to competition for light, not water stress.

Seasonal patterns of soil water potentials produced by the revised model were also examined and compared to the original model results. As the percentage of grass cover on site increased, the onset of water stress in the bottom soil layer was delayed (Figure 14). For example, the water stress in the bottom soil layer for the simulation with 10% grass began to ‘rise’ (soil water potentials became more negative) in year 15. This increase in water stress did not occur till year 25 for the simulation with 40% grass cover. This trend is associated with the point where the leaf area of the large tree component on the site is beginning to increase (refer to Figure 4). With higher levels of grass cover on the site, the development of large trees is delayed. Since root development is assumed to be symmetrical with leaf area development, trees are unable to access the water in the lower soil layer until they have grown into large trees. Figure 15 shows in more detail the development of water stress within the upper and lower soil layers for several different years as the simulated stand of small trees under 10% grass cover grows into large trees. Years 15, 19 and 25 capture the period of transition (as seen in Figure 4) where the leaf area on the site changes from being dominated by the grass and small tree components to being dominated by the large tree component. By year 30, the majority of the leaf area on the site is contributed by the large tree component. This is because 1) small trees experienced some mortality earlier, and 2) the surviving small trees grew to

be 'large' trees (> 1.3 m. in height) and 3) as large trees, they continued to grow and put on more leaf area. At the beginning of the simulation, the upper soil layer experienced the most extreme water potentials and much more variability in water potentials than the bottom soil layer. By the end of the 30-year period, the bottom soil layer was experiencing more extreme water potentials, but still showed a smooth curve with little day to day variation.

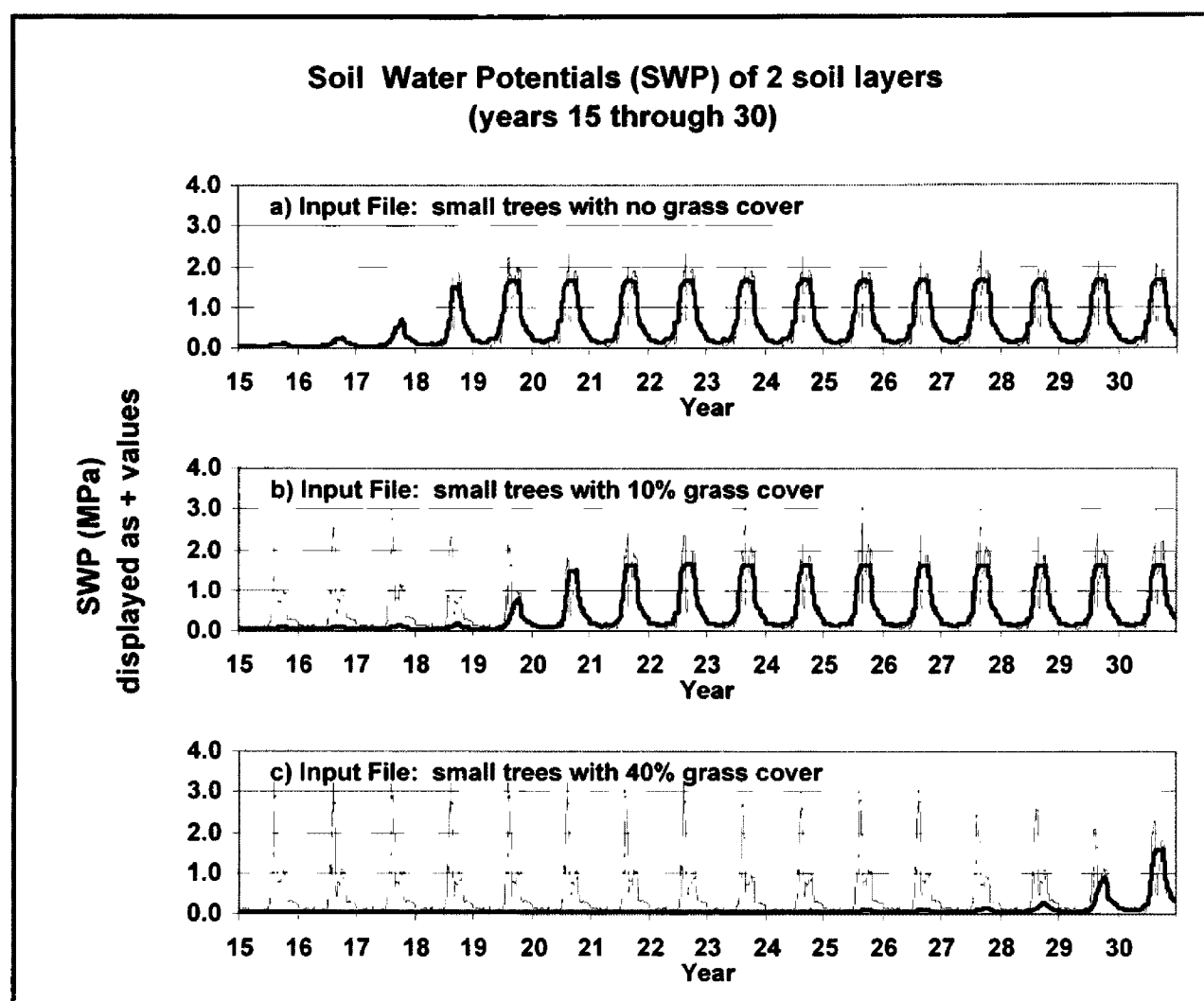
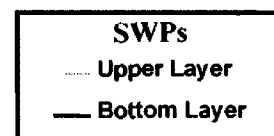


FIGURE 14. Development of moisture stress within two soil layers. Soil water potentials (SWP) are displayed as positive values from year 15 to year 30. The onset of water stress in the bottom layer is delayed as the level of grass cover is increased.



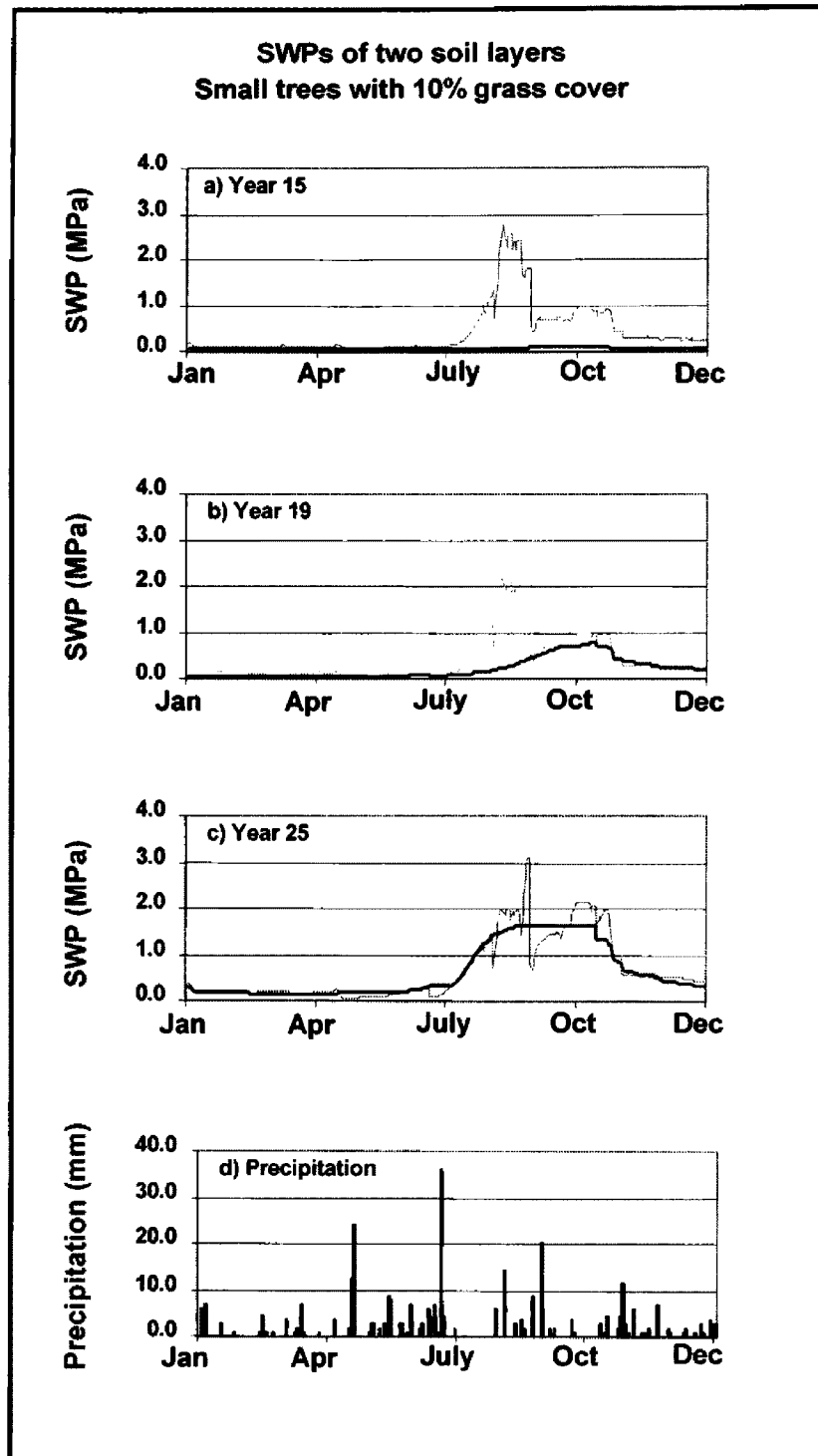
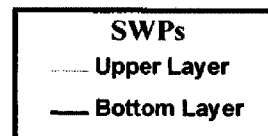


FIGURE 15. Seasonal patterns of soil moisture within two soil layers as stands develop over time (i.e., as small trees grow into big trees).

Input file for model projections consists of small trees with 40% grass cover. Soil water potentials shown as positive values (MPa) at year 15 (a), year 19 (b), and year 25 (c). Precipitation inputs are shown in d.



Water stress in the two soil layers exhibit similar patterns, peaking during the summer season (maximum soil water potentials) and showing the least water stress in winter as the soil moisture profile is recharged from snowmelt and evaporative demand is reduced. The most extreme water potentials occurred in the upper soil layer with minimum values between -2.5 and -3.5 MPa during the summer for all simulations. The bottom soil layer shows little to no water stress in the early stages of stand development when leaf area indexes are below 0.5. As LAIs increase and small trees grow to be large trees, soil water potentials in the lower soil layer begin to show the development of water stress. The top soil layer experiences larger variation in soil water potentials than the bottom soil layer. This appears to be correlated with precipitation events (see Figure 15) and also with evaporative demand.

6. DISCUSSION

For purposes of judging the behavior of the revised model, three questions were posed.

1). Does the revised model better simulate the development of small trees over time than the original model? In the original model, as 'small' trees grew into 'large' trees, their growth continued to be excessively influenced by the presence of grass on the site. In accordance with Walter's two-layer hypothesis of soil moisture partitioning (1971), a decoupling of trees from grass competition once 'small' trees become 'large' has been incorporated into the revised model with the two soil layers. That is, once small trees became large trees (greater than 1.3 m) they were better able to ignore the presence of grass. In the original model, the presence of grass suppressed tree growth, even once

the trees became 'large' trees. The revised model was more successful at decoupling, showing a steady increase in leaf area for the large tree component as the stand developed (that is, as small trees grew into large trees) even with increasing levels of grass cover on the site. In the original model projection for large trees with 40% grass cover, the maximum SWP was -2.27 MPa. In the revised model projection for the same vegetative conditions, the upper soil layer experienced more negative SWPs (-3.52 MPa). So grasses and small trees encountered more water stress in the revised model than in the original model. However, the opposite is true for 'large' trees (greater than 1.3m in height). The minimum SWP (maximum water stress) that the large trees encountered in the original model was -2.27 MPa. However, in the revised model where the large trees depend on the 'best' layer, the most extreme SWP large trees encountered was only -1.63 MPa, which is still below the leaf water potential at stomatal closure set within the model. Thus, in the revised model, grasses and small trees experience more severe water stress, while large trees experience less severe water stress than in the original model. This explains why grass production levels off at slightly lower LAI and large trees put on more leaf area and grow larger in heights and diameters with the revised model. As mentioned earlier, there is probably not a definitive transition point where trees gain access to water deeper in the soil profile. In nature, trees more probably gradually gain access to more soil resources as they grow larger and taller, not all at once when they obtain a certain height. STAND-BGC could be further modified to handle such a gradual transition by weighting the access a tree has to water depending on the tree's size.

These results indicate that the revised model which incorporates two soil layers does more successfully mimic trees escaping competition from grass as they develop into

large trees. The results from the 'large' tree stand simulations indicated that grass on the site caused some suppression of tree growth in both model versions, with revised model simulating slightly less suppression. This suggests that large trees are better able to 'ignore' the effects of grass in the revised model.

2). Does the revised model produce patterns of soil moisture that mimic the two-layer hypothesis of soil moisture partitioning? The revised model produced patterns of soil water potentials in the two soil layers consistent with Walter's two-layer theory and with what has been observed in the field. The top soil layer showed more variation, developed more extreme SWPs (more negative), due to more instantaneous reaction to precipitation inputs, evaporative demand, and transpirational demands of grasses and small trees. The bottom soil layer showed a steadier pattern with generally higher water potentials (less stress). This could be attributed to a buffering of moisture inputs and no evaporative demand. As expected, the pattern of water availability in the soil profile changed with different forest structures -- as the small trees on the stand grew into large trees.

Walter's two-layer model, whose logic has been incorporated into the revised STAND-BGC model, is broadly consistent with what is observed in nature, but many local exceptions may occur. Many woody species are quite plastic with respect to rooting patterns. Not all grasses are shallow-rooted. Sometimes, bedrock or the water table depth prevents roots from growing deeper. When in moist situations (humid savannas of Africa, (LeRoux et al., 1995) tree roots and grass roots compete directly in the upper layers. Still competing at many levels, tree roots do not entirely escape competition by going to lower soil depths, because often the available nutrients (N, P, K, Na) are found

mostly in the top soil layers. So this approach serves as an approximation only at the life form level. As more data becomes available at the individual species level, such data should be incorporated to further improve the modeling effort.

3). Since this is a model that is meant to be used in the management of forest stands, the final test of the model is whether it results in reasonable patterns of mortality and in reasonable diameter and height increments. While most of the values generated by the revised model are within a reasonable range, this is an area which needs to be more rigorously validated. There were no data sets available against which to test the model at this time. However, small tree and grass competition studies are being installed starting this summer in the inland Northwest to gather data on these situations. The results should provide a good validation data set against which to more rigorously test this revised model.

APPENDIX A

STAND-BGC Driving, Site, Life Form, and Output Variables with Their Units

Required daily inputs	Units
Day of year	
Air temperature, maximum	°C
Air temperature, minimum	°C
Relative humidity	%
Total solar radiation	kJ/m ² /day
Precipitation	cm
Daylength	sec
Maximum photosynthetically active radiation (PAR)	umol/m ² /s
Soil temperature	°C
Atmospheric CO ₂ concentration	Ppm
Atmospheric pressure	Pa
Average daylight air temperature	°C
Average night minimum temperature	°C
Average wind speed	m/s
Vapor pressure deficit	mbar
Absolute humidity deficit	ug/m ³
Canopy daily absorbed radiation	kJ/m ² /day
Site variables	
Initial soil water content	m ³ /ha
Soil depth	m
Soil water content at field capacity	m ³ /m ³
Initial Snowpack	m ³ /ha
Snowmelt coefficient	m/°C /day
Albedo	%
Percent Sand, Silt and Clay	%
Life form variables	
Maximum leaf conductance	m/s
Minimum leaf water potential	-MPa
Boundary layer conductance	m/s
Respiration: leaf, stem, coarse roots, fine roots	kgC/day at 0 C
Maximum photosynthetic rate	umol/m ² /s
Leaf turnover coefficient: leaf, stem, root	%/yr
Leaf lignin concentration	%
Specific leaf area	m ² /kgC
Life form variables, continued	
Interception coefficient	m/lai/day

Canopy light extinction coefficient (dimensionless)	
Leaf water potential at stomatal closure	-MPa
Vapor pressure deficit at stomatal closure	mbar
Optimum temperature photosynthesis	°C
Max temperature photosynthesis	°C
Growth respiration fraction: leaf, stem, coarse root, fine root	
Carbon allocation fraction: leaf, stem, coarse root, fine root	
Ratio all-sided LAI to 1-sided LAI	
Slope of GS vs PAR	mm/s
Coefficient for maintenance respiration	
Fraction of C in dry matter	kgC/kg drywt
Maximum ratio of LeafC/(LeafC +Fine_RootC)	
Water stress integral fraction	
Stem/coarse root allocation ratio	
Fraction of branches in total stem carbon	

Daily Outputs

Transpiration	m ³ /ha
Evaporation	m ³ /ha
Runoff	m ³ /ha
Soil water content	m ³ /ha
Predawn leaf and soil water potential	MPa
Site LAI	m ² /ha
Photosynthesis	kgC/ha
Maintenance respiration	kgC/ha
Growth respiration	kgC/ha

Annual Outputs

Total photosynthesis	kgC/ha
Total transpiration	m ³ /ha
Total growth respiration	kgC/ha
Total maintenance respiration	kgC/ha
Litterfall or turnover	kgC/ha
Mortality	
Carbon partitioning: leaf, stem, root	kgC/ha
Updated entity dimensions	

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